## Chapter nine

# The role of evolutionary genetics in studies of plant invasions

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## INTRODUCTION

Invasive species have long raised the interest of evolutionists, as they provide ideal systems to understand the evolutionary processes that determine and accompany the expansion of a species (Baker and Stebbins 1965). Pragmatically, invasions of non-native species or genotypes pose a major biological threat to native biodiversity and ecosystem functioning. While the ecology of these invasions has received considerable international attention, understanding the evolutionary dimensions of this problem remains rudimentary. The observation can be made however, that invasions have two main evolutionary consequences; first, they can result in the rapid evolution of introduced populations in new environments, and secondly, they can promote reticulate gene flow with related taxa at the population, ecotype, or species level (Mooney and Cleland 2001). Both processes will result in new genotype-by-environment interactions and subsequent genetic diversification.

Despite much conjecture about the genetic characteristics of invasive species, data collection has resulted in ambiguous conclusions. Allozyme data indicate *Bromus tectorum* (cheatgrass) may have a "general purpose genotype" (Novak

*M.W. Cadotte et al. (eds.), Conceptual ecology and invasion biology,* 193–221.

and Mack 1993), quantitative genetic data indicate *Sapium sebiferum* (Chinese tallow) may undergo post-introductory adaptations (Siemann and Rogers 2001), and other species may require a novel combination of intra- or interspecific genetic variation from the home range to produce a successful invader (*e.g., Tamarix* species, Gaskin and Schaal 2002).

It is becoming clear that invasions can result in rapid evolutionary events via a number of genetic mechanisms (Ellstrand and Schierenbeck 2000; Lee 2002). The recent development of genetic and genomic approaches has allowed the investigation of model or cultivated systems at the sequence level. Data have accumulated rapidly in the past few years to elucidate molecular level mechanisms that promote species formation and expansion (Rieseberg and Wendel 2004). Among the questions that can now be addressed are (1) the geographic and evolutionary origin of invasive species (2) the identification of the parental genotypes that are involved in the formation of new (recent) invasive species (3) the possible genetic exchanges between invasive and native species (4) genome evolution of invasive species compared to related non-invasive species (5) the molecular basis of adaptive traits that may promote invasiveness (6) importance of neutral versus adaptive processes that have accompanied genome evolution of invasive species.

Allendorf and Lundquist (2003) and Lee (2002) are among those that emphasize that genetic considerations should play a larger role in the development of invasive species management and control. Sadly, adequate genetic data rarely exist to set policy at a regional or global level. We hope to compel the reader of this chapter that the genetics of invasive species are interesting and important from a theoretical evolutionary perspective and merit fundamental consideration at the management level. Researchers just entering the study of evolutionary genetics can be assured of many decades of work with invasive species at the molecular, population, or species level. However unfortunate the circumstance, species invasions are ideal for the provision of syntheses between ecology and genetics.

## ROLE OF MOLECULAR EVOLUTION IN INVASIVE ABILITY

Possible heritable factors that contribute to invasive ability have been conjectured since Darwin (1872). Although sophisticated techniques to explore the genetics of invasive ability are now available, the field still has far to go to find practical methodologies to elucidate the complex genetic and ecological interactions of invasive species. Whether invasive plant species are "born or made" (Ellstrand and Schierenbeck 2000), if a particular genetic characteristic is identified, we can now determine whether allelic variability for a trait exists and assess its evolutionary importance in synthesis pathways or gene expression.

As agricultural weed scientists realized over 60 years ago, weed control, genetics, and molecular biology are basically and intimately related via studies on chemical disruption of complex metabolic pathways (Gressel 2000). As a result of enzymes that are blocked by herbicides, the pathways in which they occur become elucidated and may subsequently become important in transgenic experimentation (Gressel 2000). Of particular note, agricultural scientists use basic evolutionary principles when faced with the often inevitable resistance problems that result from herbicide use. For example, the herbicide paraquat has been successful in a "pretest" for a genetic predisposition for transient drought tolerance because both drought and herbicide resistance cause oxidative stress (Gressel 2000). Tests for screening favorable genotypes in crop situations may be useful in screening unwanted non-native horticultural genotypes that may contain traits such as resistance to drought stress that are known to contribute to invasiveness (Bazzaz 1986). An important step in the development of a management policy of invasives is the integration of techniques that are flexible enough to respond to genetic traits that may change as a result of adaptation and control. The role of the ecologist and land manager should not be underestimated in the determination of the ecological importance of the genetic traits of invaders.

We considered five major aspects of the role of molecular evolution to invasive ability. First, the genetic variability necessary to respond to new environmental pressures exists within some taxa, *i.e.*, either "untapped" genetic variation or a "general purpose genotype" (Baker 1965). Secondly, more rapid evolution can result from adaptive radiation into uninhabited niches, similar to that found with adaptive radiation in island ecosystems. Depending on age and disturbance history, some of these niches may be more available than others and thus become receptacles for rapid evolutionary change. Our third topic considers an idea hypothesized upon for many years (Stebbins 1950), mainly that polyploidy may create an advantage in invasions due to molecular evolution of gene duplications and increased genetic variation. Fourth, the creation of new variation can result from hybridization at either the inter- or intraspecific level and this genetic variation can originate from repeated introductions and seed banks. Lastly, not all aspects of the evolution of invasive species result from genetic variation; insights have recently accumulated, that stress the importance of epigenetic mechanisms and the role of expression plasticity in shaping phenotypes.

## Existing genetic variation

### *Molecular Genetics*

Questions regarding the importance of molecular markers to measure response to selection are part of the larger debate over "nearly-neutral" versus selectionist theory (Ohta and Gillespie 1996). If the question is, 'is the heterozygosity of molecular markers necessary for a response to selection?', the answer is a qualified "no". Reed and Frankham (2001) have gone as far as to suggest that genetic diversity data have little place in the context of the invasive species question. Despite this view, a number of examples demonstrate that variable molecular markers can be useful in understanding plant invasions. Genotypes that are clearly more invasive than others have been identified in *Tamarix* (salt cedar) species

(Gaskin and Schaal 2002) and *Phragmites australis* (common reed) (Saltonstall 2002). In addition, we are now able to identify variation in chromosomal regions, if not for particular genes, that confer a fitness advantage in invasions. Clauss and Mitchell-Olds (2003) have demonstrated a direct relationship between trypsin inhibitor loci, important in plant defense in *Arabidopsis* (mouse-ear cress), and the evolution of life history traits. A quantitative trait locus in *Helianthus paradoxus* (pecos sunflower) suggests Ca-dependent salt tolerance and higher fitness in a range of environments in the hybrid species (Lexer *et al.* 2003). Although admittedly there is much to learn about the relationship between the molecular genetic variation of populations and selection, it remains a fruitful and seminal area of inquiry, particularly with plant invasions.

Genetic markers are often used in selection and other genetic manipulations of agricultural crops (Dekker 2003). Basic population genetics have been useful in the separation of two hybridizing *Amaranthus* (pigweed) species to prevent the introgression of transgenics (Wetzel *et al.* 1999). Molecular markers have been useful in *Oryza* (rice) species in the identification of varieties that may or may not be able to hybridize and subsequently whether these varieties are appropriate for a particular growing region (Cohen *et al.* 1999). The similar application of such markers to invasive species will lead to removal prioritization of problematic genotypes in particular geographic regions, assuming they can be visually differentiated in the field.

One of the problems with using existing genetic variation as an explanation for invasive ability is that it often requires widespread and intensive sampling from both the native and introduced ranges. The most definitive work in the comparison of native and introduced genotypes is with *Bromus tectorum* (Novak and Mack 1993, Novak *et al.* 1993; Bartlett *et al.* 2002). *Bromus tectorum* is a cleistogamous plant with various homozygous multilocus genotypes; repeated introductions of different Old World genotypes that have invaded North America have resulted in the redistribution of the genetic diversity available in the native area of the species. Although the *B. tectorum* work is very thorough, further data collection is needed to determine whether predictions can be made about invasive *B. tectorum* genotypes. Broad tolerances needed for phenology, seed set, drought, and freezing are found in *B. tectorum* and obviously these traits have some genetic basis. For species like *B. tectorum* that have reduced genetic variation, the ideal match between invader characteristics and new range environment may be simply idiosyncratic, *i.e.*, a genotype is "pre-adapted" for the new range. On the other hand, millenia of selective processes and inbreeding in *B. tectorum* may have worked together to result in the "ideal invader". These are the "general purpose genotypes" of Baker, genotypes that can grow in a variety of different environments, with no need to undergo further selection (Williams 1992).

There remains a lack of consensus regarding the relationship of genetic variability to the invasive ability of plants, *i.e.*, some invasive species maintain low levels of genetic variation (Baumel *et al.* 2001; Ye *et al.* 2003) whereas others are highly variable (Barrett and Richardson 1986). Despite conjecture on this matter since 1965 (Baker and Stebbins 1965), experimental evidence in this area has been slow to accumulate. A number of authors have found that invasive species with low levels of genetic diversity often share traits such as inbreeding or an annual life habit with a self-breeding system (Brown and Marshall 1981, Warwick, 1990, Novak and Mack 1993, Wang *et al.* 1995, Squirrell *et al.* 2001, Bartlett *et al.* 2002). These conclusions, as with many other conclusions about invasive species, have exceptions, for example *Viola riviniana* (common dog violet), is a primarily clonal, cleistogamous species with high levels of genetic variation (Auge *et al.* 2001).

Grouping species by life history traits and geographical range has been successful in detecting association between genetic diversity and life history characteristics for plant species in general (Hamrick *et al.* 1979; Loveless and Hamrick 1984; Hamrick *et al.* 1992). Thus, it maybe useful to first categorize invasive species by life history traits and then look for patterns in genetic diversity (Schierenbeck *et al.* 1995). Hamrick *et al.* (1979) found that weedy and early successional species are less variable than species of mid- and late-successional stages. A recent study with the herbaceous perennial, *Alternanthera philoxeriodes* (alligator weed, a native of South America) supports this pattern. Considered one of the world's worst weeds, *A. philoxeriodes* is a partially submerged aquatic with widespread clonal propagation and very low genetic diversity throughout southern China ($H_T = 0.0286$, Xu *et al.* 2003).

Among long-lived woody species for which genetic variation has been measured, correlations between life history traits and genetic variation are less clear and for most studies on invasive woody angiosperms, genetic variation is reported for the home range only. For example, there are home range studies for *Robinia pseudoacacia* (black locust) (Surles *et al.* 1980), *Prosopis glandulosa* (honey mesquite) (Paneida and Carstairs 1989), *Casuarina cunninghamiana* (river-she oak) (Moore and Moran 1989), *Acacia melanoxylon* (blackwood wattle) (Moran *et al.* 1989), *Acacia decurrens* (green wattle) (Moran *et al.* 1989), and *Eucalyptus obliqua* (messmate) (Brown *et al.* 1975) and all show higher levels of variation than expected for species with similar life history traits (Schierenbeck *et al.* 1992). All but one of these species (*Eucalyptus obliqua*) are nitrogen fixers and it should be noted that the trait for nitrogen fixation is well-associated with ability to invade new ranges rapidly (Vitousek 1986). *Lonicera japonica* (Japanese honeysuckle) an invasive woody vine native to Asia and invasive throughout warm temperate and tropical climates worldwide, has levels of variation within the range expected for species with similar life history traits (Schierenbeck *et al.* 1995). An invasive clonal vine of the southeastern U.S., *Pueraria lobata* (kudzu) has a high level of genetic variation in its introduced range that is suggestive of multiple introductions. Excess heterozygosity in introduced populations of *P. lob*ata also suggests that selection may be act in favor of heterozygous individuals (Pappert *et al.* 2000). *Rubus alceifolius* (giant bramble), a shrub native to southeast Asia, has greater genetic variation in its home range, reduced variation in its new range of Madagascar, and a single invasive genotype as measured by

AFLPs, in its new range in the Indian Ocean (Amsellem *et al.* 2000). In a more recent example, DeWalt (2003) found *Clidemia hirta* (soapbush), a shrub native to Central and South America and invasive in Hawai'i, had low levels of genetic variation in both the introduced and home range. Surprisingly, to our knowledge, there are no more recent reviews that examine the relationship between genetic variability, invasiveness, and life history traits.

Regardless of the expectations of genetic variability in native or introduced populations, effective studies of intraspecific genetic variation require the use of a number of genes. Coalescence analyses of gene genealogies allow a determination of the geographic origins of invasive genotypes (Gaskin and Schaal 2000; Schaal *et al.* 2003) and the expansion of genotypes during invasion can be retraced through star-like phylogenetic patterns that indicate recent and rapid population growth (Slatkin and Hudson 1991). Although haplotype phylogenies are useful in the reconstruction of historical and recent gene flow patterns, the analytical techniques for the determination of historical gene flow patterns have only recently become available (Templeton 2004). Complications can arise however, in hybrid lineages that form new, recombining, coaslescent complexes.

### *Quantitative Genetics*

The long-term conjecture that certain traits are associated with invasiveness (Baker 1965, 1974; Bazzaz 1986) is now supported by experimental evidence for the genetic basis of phenology in *Capsella bursa-pastoris* (shepard's purse) (Neuffer and Hurka 1999), *Solidago altissima* (tall goldenrod), *S. gigantea* (late goldenrod) (Weber and Schmid 1998), high relative growth rates and early reproduction for *Pinus* (pine) spp. (Rejmanek and Richardson 1996; Grotkopp *et al.* 2002), and trade-offs between herbivore defense and fitness (Strauss *et al.* 2002). Parker *et al.* (2003) concluded based on measured growth rates, freezing tolerance, and growth habits, that the invasiveness of *Verbascum thapsus* (mullein) is more likely due to a general purpose genotype that is influenced more by environmental conditions than by heritable factors.

A small number of quantitative genetic studies of native and introduced genotypes have found post-colonization evolution of genetic traits. For example, in *Sapium sebiferum,* introduced populations had a greater seed set than native populations but less protection from herbivory (Siemann and Rogers 2001). Leger and Rice (2002) found selection within 150 years for genetically based growth and reproductive traits in genotypes of the California native *Eschscholzia californica* (California poppy), invasive in Chile.

Lee (2002) suggests invasive ability may be more of reflection of ability to respond to selection than to phenotypic plasticity; but this leads us back to the question of whether invasive species are born or made, and definitive data with which to answer this question simply do not exist.

### Rapid evolution resulting from adaptive radiation

Adaptive radiation, in the classical sense, is the colonization and subsequent diversification of species from a common ancestor into new habitats. The process of adaptive radiation, in part, inspired Darwin's theory of natural selection and has been supported empirically for at least four decades at many spatial and temporal scales. The recent spread, radiation, and evolution of invasive species likely follows similar processes of adaptive radiation. Questions remain, however, about the rapidity and spatial scale with which this process can occur. Can fragmented, disturbed landscapes devoid or partially devoid of native biota be considered island situations and receptacles for adaptive radiation? We know virtually nothing about what evolutionary processes will occur in situations in which species from remote areas of the globe are brought together into a new habitat. The human mediated migration of propagules is not unlike non-human mediated dispersal, although on a different temporal scale. Reznick and Ghalambor (2001) reviewed 47 studies to conclude that the rapid evolution following colonization of new habitats is promoted by new ecological conditions. Novel ecological conditions in their study included new food resources, biotic or abiotic interactions, predators, and competitors. Species poor communities that subsequently became vessels for rapid evolutionary change often were a result of anthropogenic disturbance (Reznick and Ghalambor 2001). We know of no work which has examined the rapid evolutionary consequences of dispersal of a single plant species into a range of new and different habitats, although there are some animal examples (Huey *et al.* 2000, Losos *et al.* 1997). We primarily can draw from examples which illustrate the rapidity with which evolution can occur following adaptive radiation.

Classic examples of adaptive radiation in island habitats are not only examples of rapid evolutionary change but provide ideal opportunities to study the genetics and ecology of invasions. An example of very effective colonization into new, unoccupied habitats has been well-supported in the magnificent diversification of the Hawaiian silversword alliance over the last 6 million years (Barrier *et al.* 1999; Barrier *et al.* 2001). Comparisions of mutation rates between genes important in the regulation of floral and inflorescence development and non-regulatory genes in the Hawaiian silversword alliance provide evidence that adaptive radiation may be more correlated with variation in regulatory loci (Barrier *et al.* 2001).

Reticulate gene flow can facilitate adaptive radiation via new gene combinations (Seehausen 2004). If reticulate gene flow is important in the spread of colonizing species, any gene flow needs to occur prior to the spread, but there could be repeated opportunities for this to happen through repeated introductions. Support of hypotheses for rapid adaptive radiation requires variation at function loci and multiple "opportunities" for adaptive divergence with repeated introductions (Seehausen 2004). Thus a combination of repeated introductions, new gene combinations and unoccupied or partially filled niches result create a vulnerability to invasion from previously unseen genotypes. The human-mediated adaptive radiation of plant species into new habitats provides an ideal situation for the experimental study of human induced evolutionary change. However, high rates of human-facilitated plant dispersal may also prevent or slow radiation by promoting gene flow and panmixis.

### Hybridization

The prevalence of reticulate evolution, that is, the merging of divergent genomes through interspecific gene flow is known as an important evolutionary force in plants (Anderson and Stebbins 1954). The use of molecular markers has greatly helped to document origins and occurrence of hybrid lineages and the genetic consequences of introgressive hybridization (Rieseberg 1997; Arnold 1997). Molecular phylogenetic approaches that combine multiple sequence data sets have allowed the detection of ancient introgression events and reveal that reticulation is even more frequent than previously thought (*e.g.*, Doyle *et al.* 2004; Cronn and Wendel 2004; Small *et al.* 2004).

Hybridization is related to invasion in two ways: First, introduced invasive plants may hybridize with native species, and give rise to new successful and rapidly expanding taxa (Abbott 1992, Abbott *et al.* 2003). Second, hybridization between non-invasive species can result in new aggressive hybrids that compete with the parents and invade new habitats (Rieseberg and Wendel 1993). Genetic introgression between invasive species and closely related natives may have critical and rapid evolutionary consequences (Huxel 1999). The saltmarsh species *Spartina alterniflora* was deliberately introduced from the Atlantic American coast to California where it hybridized with the native *S. foliosa* (Daehler and Strong 1997). Hybridization was shown to occur in both directions, although the introduced species has higher male fitness (Antilla *et al.* 1998). Rather than suffering from competition with *S. alterniflora*, *S. foliosa* is now threatened by introgressant hybrids that result from recurrent backrosses, and that threaten the genetic integrity of the native species (Ayres *et al.* 2000). Pollen swamping is also thought to have represented an important mechanism allowing hybridization and invasion in oaks (Petit *et al.* 2004).

Human activities have increased ecologically disturbed areas, bringing together previously isolated taxa and generating open arrays of niches that are better suited to hybrids than to their parents (Ellstrand and Schierenbeck 2000). Hybrids do well in disturbed habitat (Anderson 1949) and invasive species are empirically associated with disturbed ecosystems (Vitousek 1986). This is particularly well-illustrated in the two classical examples of introgressive hybridization and hybrid speciation in the Louisiana irises (Anderson 1949, Arnold 1997) and in *Helianthus* species (sunflowers) (Rieseberg *et al.* 2003). Hybridization and introgression between *Iris hexagona* and *Iris fulva* occur primarily in disturbed areas that allow sympatry between the parental species. Hybrid genotypes display various combinations of parental ecological traits, such as shade tolerance that confer different fitnesses across different environments (Arnold 2004 and references therein). Studies on the *Iris fulva* x *I. brevicaulis* complex have also demonstrated the importance of considering all life stages in experimentation to understand hybrid evolution (Johnston *et al.* 2003). *Helianthus* is a genus particularly affected by reticulate evolution involving introgressive hybridization and homoploid hybrid speciation, as illustrated by *H. annuus* and *H. debilis* (Kim and Rieseberg 1999). Additionally, hybridization between *H. annuus* and *H. petiolaris* gave rise to three homoploid hybrid species (*H. anomalus*, *H. deserticola, H. paradoxus*); these stable new lineages diplay novel ecological adaptations. Transgressive segregation has resulted in extreme phenotypes in these *Helianthus* species and is thought to be the key for their ability to invade novel habitats (Rieseberg *et al.* 1999), *e.g.*, as demonstrated with salt adaptation in the hybrid species *H. paradoxus* (Lexer *et al.* 2004).

There are now many examples in which hybrid genotypes are more fit than one or both of the parental genotypes (Burke and Arnold 2001). Ellstrand and Schierenbeck (2000) found 28 examples in which the occurrence of new invasive taxa ness was preceded by hybridization and for which there was strong molecular evidence. Gaskin and Schaal (2002) provide both nuclear and cpDNA evidence that the most common invasive haplotypes of the voracious *Tamarix* in the U.S. are post-introduction hybrid combinations between primarily *T. ramosissima* and *T. chinensis* with some additional gene flow from *T. parviflora* and *T. gallica.*

Birchler *et al.* (2003) suggest that regulatory gene allelic interaction in hybrid genotypes might account for the well-known heterosis effect, *i.e.*, hybrid heterozygosity results in greater vigor, biomass, speed of development, and fertility than in the parental genotypes. For instance, upregulation of housekeeping genes may cause gene expression that is different in hybrids than the midparent predictions. Future studies, linking phenotypic changes and investigations at the genome level should provide new insights into molecular mechanisms that are involved in the adaptive success of hybrid lineages.

There is now little doubt that hybridization is an important evolutionary mechanism in plants, and the concern with hybridization in invasive species is not whether it can happen, but the speed with which humans accelerate this evolutionary process. Homogenization is a process that is occurring not only at the community level but also at the genetic level within taxa (Olden *et al.* 2004). Locally adapted genotypes are becoming lost through homogenization and invasion of dominants.

## Polyploidy

Polyploidy, resulting from whole genome duplication, is a widespread evolutionary phenomenon and a common speciation mechanism in plants (Stebbins 1950, Lewis 1980, Grant 1981). One of the most conspicuous contributions that has resulted from the development of recent genomic approaches is the awareness of the prevalence of polyploidy in most eukaryotic lineages (*e.g.*, Wolfe 2001; Blanc *et al.* 2003). This has contributed to a renewed interest in the evolutionary success and potential selective advantage of genome duplication (Otto and Whitton 2000).

Many polyploid species are well-adapted, successful weedy species, which reinforces the idea that polyploidy may have predisposed species to become invaders (Brown and Marshall 1981, Barrett and Richardson, 1986). Interestingly, newly formed polyploids are frequently invasive species, which suggests that polyploidy confers an immediate ecological aptitude to invade new habitats. Invasive species of recent origin are excellent model systems to investigate the early evolutionary mechanisms associated with invasiveness, and provide the unique opportunity to compare the new lineage to its parents that are generally identified and still extant. The allopolyploids *Spartina anglica* (cordgrass) (Aïnouche *et al.* 2004a), *Tragopogon mirus* and *T. miscellus* (goatsbeard) (Soltis *et al.* 2004), *Senecio cambrensis* (Welsh ragwort) and *S. eboracencis* (Abbott and Lowe 2004), and *Cardamine schulzii* (bittercress) (Urbanska *et al.* 1997) formed during the last 100-120 years, have well-documented origins, have spread rapidly, and display a larger ecological amplitude than their progenitors. These species are either perennials or annuals-biennials and display various breeding or pollination systems.

Genome duplication may have different impacts on fertility and modes of inheritance that is dependent on chromosome behavior and genetic segregation. It is generally predicted that duplication of the same genome within species (*i.e.*, strict autopolyploidy) will result in random pairing (polysomic inheritance at duplicated loci), irregular meiosis, and thus limited fertility, whereas the duplication of more differentiated (homoeologous) genomes (*i.e.*, allopolyploidy) will result in preferential chromosome pairing (bivalents), regular meiosis, high fertility and disomic inheritance (Da Silva and Sobral 1996). In fact, autopolyploids and allopolyploids occur on a continuum in nature, as the ongoing evolutionary process results in more or less divergent parental populations of the polyploid (Stebbins 1971; Wendel and Doyle 2004). Moreover, chromosome pairing may be affected by various genetic and genomic factors and vary with the age of the polyploid; it is then recommended to distinguish between the mode of formation of a polyploid species and its mode of chromosomal segregation (Otto and Whitton 2000).

Recent research has resulted in a particularly dynamic vision of polyploid genomes over both a short- and long-term evolutionary time scale (Wendel 2000, Soltis and Soltis 2000). The development of molecular markers and particularly, the combined use of maternally-inherited cytoplasmic markers with biparentally-inherited nuclear markers has allowed the detection of multiple and recurrent origins of polyploid species (Soltis and Soltis 1999). As multiple-sequence datasets are now available for phylogenetic analyses, it is possible to detect recurrent and bi-directional reticulate evolution even in old polyploid lineages (*e.g.*, *Glycine* Doyle *et al.* 2004) where they otherwise would have been undetected.

The process of recurrent polyploid formation with reticulate gene flow may involve various parental genotypes and increases the level of genetic diversity available to newly formed species (Schierenbeck *et al.* 1992). For instance, at least 21 lineages of separate origins for the allotetraploid *Tragopogon miscellus* and 11 for *T. mirus* have been documented in the Palouse according to various morphological and molecular (allozymes, chloroplast and nuclear DNA) lines of evidence (reviewed in Soltis *et al.* 2004); these recurrent origins involve either only one diploid species as the maternal parent (*e.g.*, *T. porrifolius* for the allotetraploid *T. mirus*) or alternatively both the parental species *T. porrifolius* and *T. dubius* in reciprocal crosses (*e.g.*, for the allotetraploid *T. miscellus*). This has resulted in various genotypes and dramatic floral differences in the allopolyploid populations that are progressively replacing diploids as prevalent weeds (Soltis *et al.* 2004). Similarly, two separate origins have been documented in North Wales and Scotland for the ruderal allohexaploid *Senecio cambrensis* that originated in Britain during the past 85 years (reviewed in Abbott and Lowe 2004). One of the most complex examples of multiple allopolyploid origins is represented by the polyploid agamic complex *Antennaria rosea* (pussytoes) that has formed from multiple crosses involving various diploid taxa occurring in specific habitats of the Rocky Mountains (Bayer 1997). The polyploid lineages of this "compilospecies" are gametophytic apomicts that display larger ecological amplitude than their diploid progenitors.

Not all successful allopolyploids have multiple origins. In contrast to *Tragopogon* spp., *Sencecio cambrensis* and *Antennaria rosea*, the invasive saltmarsh species *Spartina anglica* has undergone a severe genetic bottleneck at the time of its formation in the Bay of Southampton (U.K.). This dodecaploid species formed after chromosome doubling of the first generation hybrid *Spartina x townsendii* that has resulted from hybridization between the introduced East-American hexaploid *Spartina alterniflora* and the native hexaploid *Spartina maritima* (Raybould *et al.* 1991). Both parental species lack genetic diversity in the hybridization site; a limited number of *S. alterniflora* genotypes have been introduced in Western Europe (Baumel *et al.* 2003), whereas a striking lack of molecular variation is encountered in populations of the native *S. maritima* (Yannic *et al.* 2004). European populations of *S. anglica* are mostly composed of one major multilocus genotype that has formed in Southampton, and that is identical to the first generation hybrid *S. x townsendii* (Baumel *et al.* 2001; 2002a). Chloroplast DNA analysis has revealed all populations of *S. anglica* in western Europe display identical plastome to *S. alterniflora* which is then considered as the maternal genome donor (Ferris *et al.* 1997; Baumel *et al.* 2001). *Spartina anglica* has rapidly invaded the British saltmarshes since its formation (Thompson 1991) and it has been naturally or deliberately introduced in various continents (such as China or Australia) where it is now considered as a serious threat to native flora and fauna (Aïnouche *et al.* 2004a and references therein). Although it has limited inter-individual genetic diversity, *S. anglica* contains two well-differentiated homoelogous genomes inherited from its hexaploid parents, which provides fixed heterozygosity at homoeologous loci (Baumel *et al.* 2002b; Aïnouche *et al.* 2004b). *Spartina* is an ideal system in which to explore the genetic and genomic consequences of hybridization and gene duplication in successful invasive species; although previous attempts of re-synthesizing experimentally the allopolyploid have failed, time since species formation and the parental species are known; it is possible to differentiate between the effects of hybridization (in. *S. x townsendii*) and genome duplication (in *S. anglica* populations); moreover, two natural replicates of hybridization events between *S. martima* and *S. alterniflora* are available in *S. x towsendii* and *S. x neyrautii* another hybrid that has formed at the same period in southewest France, with no genome doubling (Baumel *et al.* 2003).

The immediate consequence of polyploidy is a greater intra-individual genetic diversity and heterozygosity at duplicated loci than in diploids that results in increased biochemical diversity (Roose and Gottlieb 1976) and confers a greater tolerance to environment variation and may promote successful colonization (Brown and Marshall 1981). Gene duplications resulting from polyploidy are also believed to have a buffering effect against deleterious mutations (Ohno 1970, Lynch and Conery 2000, Lawton-Rauh 2003). Additionally, polyploids of hybrid origin (allopolyploids) may benefit from higher fitness due to heterosis. Similarly, traits which result in the "gigas" effect, or a general increase in morphological characteristics (de Vries 1905), are associated with both polyploidy and invasive plant species (Baker 1974; Rieseberg *et al.* 1999). *Hypericum perforatum* (St. John's wort), a tetraploid thought to be of allopolyploid origin, has high reproductive plasticity (Matzke *et al.* 2001) but reproduces most commonly via facultative apomixis. Field collections of *H. perforatum* in Australia found a lack of within population variation (Mayo and Langridge 2003) but high interpopulational genetic diversity. *Hypericum perforatum* has high levels of hypericin, a chemical that causes photosensitization and reduced herbivory, that are hypothesized to be a direct result of allopolyploidization (Mayo and Langridge 2003). Introduced into North American in the 1920s, the allopolyploid and nearly monomorphic *Setaria faberi* (giant foxtail) is now present throughout the disturbed areas on the continent (Pohl 1951, 1966; Hafliger and Scholz 1980). Dekker (2003) named the allopolyploization of *S. faberi*, the "weed speciation event", as the polyploid has higher fitness in agricultural systems than its diploid ancestors. One of the world's worst weeds is the polyploid *Sorghum halepense* (Johnson grass), a product of hybridization between the cultivar *S. bicolor* and the wild *S. propinquum*, and which responds well to cultivation and is extremely pernicious to due the rhizomatous growth habit (Paterson 2002).

A growing body of evidence continues to accumulate in regard to the dynamic and plastic nature of polyploid genomes that would explain their evolutionary success. Allopolyploid genomes are particularly dynamic at both the structural and expression levels over the long- and also short-term evolutionary time scale (reviewed in Wendel 2000, Liu and Wendel 2002, Osborn *et al.* 2003). Significant advances in revealing the occurrence and nature of the early evolutionary changes in polyploid genomes are possible due to experimentally resynthesized allopolyploids involving well-known model systems such as *Brassica* (oilseed rape), *Arabidopsis*, *Gossypium* (cotton), or *Triticum-Aegilops* (wheat). These model systems allow the exploration of allopolyploid material of known origin with the comparison of their actual parental genotypes, a condition rarely met for most natural allopolyploids. Rapid and biased structural changes have been encountered in the first generations following polyploidization in *Brassica* (Song *et al.* 1995) and wheat (Feldman *et al.* 1997; Liu *et al.* 1998a, 1998b, Ozkan *et al.* 2001). However, Liu *et al.* (2001) did not find consistent structural changes in newly synthesized allopolyploid *Gossypium*. Various evolutionary mechanisms appear to affect allopolyploid genomes over a longer term and include: the independent evolution of duplicated genes in allotetraploid cotton that formed one to two million years ago (Cronn *et al.* 1999, Senchina *et al.* 2003); interaction between the homoelogous subgenomes for repetitive sequences *via* concerted evolution (*e.g.*, *Gossypium*, Wendel *et al.* 1995, *Nicotiana* (tobacco), Volkov 1999); or spread of transposable elements (Zhao *et al.* 1998). The fate of duplicated homoeologous genes has been particularly well-investigated in the *Gossypium* system by Jonathan Wendel and his colleagues (*e.g.*, *ADH* genes, Small and Wendel 2000, 2002; *MYB* genes, Cedroni *et al.* 2003) and reveals various evolutionary patterns including copy number lability, pseudogenization, gene elimination, or accelerated rate of nucleotide substitution (*e.g.*, for *ADH-C* genes). However, a recent analysis of 48 nuclear genes (Senchina *et al.* 2003) indicated that polyploidy led to an overall modest enhancement in rates of nucleotide substitution in *Gossypium.*

When compared to resynthesized allopolyploids, naturally nascent allopolyploids display different patterns of genome evolution; various levels of concerted evolution seem to have affected rDNA sequences of the young allopolyploid populations in *Tragopogon* (Soltis *et al.* 2004), whereas no homogenization of the parental sequences is observed in *Spartina anglica* (Aïnouche *et al.* 2004a). In the latter system, no major change of the parental genomes are observed for various multilocus markers (ISSRs, RAPDs, AFLPs), although some preferential loss of maternal (from *S. alterniflora*) AFLP fragments are observed in *S. x townsendii* and *S. anglica* (Aïnouche *et al.* 2004b, Salmon A. *et al.* unpublished). A transposon display analysis indicates no burst of retro-element activation in *S. anglica* (Baumel *et al.* 2002a) and suggests that different biological systems respond variously to polyploidy (Liu *et al.* 2001). In spite of the structural genomic stasis encountered for most of the markers investigated to date, *Spartina anglica* populations exhibit consistent morphological plasticity (Thompson 1990), and suggest a probable functional plasticity in the expression of the duplicated loci (Aïnouche *et al.* 2004a).

Recent studies have pointed out that there is modulated expression of duplicated loci in polyploids (Comai 2000, Shaked *et al.* 2001, Kashkush *et al.* 2002, Kashkush *et al.* 2003, He *et al.* 2003, Adams *et al.* 2003). These expression changes may involve various mechanisms, including increased variation in dosage-regulated gene expression, altered regulatory networks, and genetic or epigenetic changes (Riddle and Birchler, 2003; Osborn *et al.* 2003). In wheat, polyploidy was accompanied by transcriptional activation of retroelements that led to novel expression patterns (Kashkush *et al.* 2003; Levy and Feldman 2004). Expression changes may have profound impact on fitness when they result in variable phenotypes. Gene silencing resulted in phenotypic variation and instability in experimentally resynthesized *Arabidopsis* allotetraploids that displayed considerable variation in morphology, flowering time, and fertility (Comai *et al.* 2000).

Novel flowering time variation was also observed in resynthesized allopolyploid *Brassica napus* (Schranz and Osborn 2000). Expression of 40 homoeologous gene pairs was analysed by Adams *et al.* (2003) in natural (1 to 2-myr old) and synthetic allotetraploid *Gossypium*. The duplicated genes showed unequal levels of expression and organ-specific reciprocal silencing, suggesting a partitioning of the ancestral functions as both immediate (in synthetic polyploids) and long-term (in natural polyploids) responses to polyploidization. In recently formed natural allopolyploids, such expression changes appear to take place also, as revealed by cDNA AFLP investigations in *Tragopogon* where about 5% of the genes examined in the allopolyploids have been silenced and an additional 4% exhibit novel gene expression relative to their diploid parents (Soltis *et al.* 2004).

### Epigenetic changes associated with invasive ability

Epigenetics refers to heritable changes in phenotype that do not result from changes in gene sequence but rather from regulatory mechanisms of gene expression (Wolffe and Matzke 1999). These mechanisms are known to be involved in growth and development (Finnegan *et al.* 2000), and can result in various morphological changes including flower structure (*e.g.*, Cubas *et al.* 1999; Comai *et al.* 2000). Such mechanisms have important evolutionary consequences because they increase phenotypic plasticity, which in turn buffers environmental pressures on genotypes. This may be astonishing to our naïve perspective of genomic interactions, but epigenetic processes are proving to be predictably associated with the structural limitations of genomes. Epigenetics is consequently becoming a very active field of research in evolutionary genomics (reviewed in Finnegean *et al.* 1998; Comai 2000; Liu and Wendel 2003).

Mechanistically, epigenetic changes result from various interacting processes, which include cytosine methylation of DNA (Martienssen and Colot 2001), histone deacetylation (Tian and Chen 2001), and short RNAs (Mette *et al.* 2000) that modulate gene silencing. Epigenetic alterations are known to be triggered by environmental stress (Finnegan 2001), and in some cases are viewed as genome defense mechanisms (Yoder *et al.* 1997; Matzke *et al.* 2000). In introgressed hybrid rice plants, Liu and Wendel (2000) observed retrotransposon activation that was rapidly repressed by cytosine methylation.

The reunion of two divergent genomes in the same nucleus in hybrid and allopolyploid species may be considered as a genomic stress that generates epigenetic changes altering gene expression and phenotypes (Comai *et al.* 2003). In synthetic *Arabidopsis* allotretraploids, Comai *et al.* (2000) observed that about 1% of the genes were silenced compared to their parents. The silenced genes were both normal genes or genes related to transposons. These changes were further found to be related to methylation modifications that were associated to phenotypic instability (Madlung *et al.* 2002). Similar levels of silencing, related to cytosine methylation, were also encountered in the corresponding natural allotetraploid *Arabidopsis suecica* (Lee and Chen 2001). In experimentally re-synthesized allopolyploid wheat, 13% of the loci investigated using Methylation Sentitive AFLP (MSAP) were found methylated (Shaked *et al.* 2001), and transcriptional activation of retrotransposons was shown to alter the expression of adjacent genes (Kashkush *et al.* 2003; Levy and Feldman 2004). Although no changes in methylation patterns were observed in newly synthesized *Gossypium* allopolyploids (Liu *et al.* 2001), the organ-specific and reciprocal gene silencing found by Adams *et al.* (2003) is interpreted as resulting from epigenetic regulation through mechanisms that have yet to be elucidated (Adams and Wendel 2004).

*Spartina anglica*, is to our knowledge, the first invasive species that has been investigated in the context of epigenetic gene expression. Aïnouche *et al.* (2004b; Salmon *et al.* 2005) have attempted to differentiate between the genomic consequences that result from hybridization and those that result from genome duplication. This was made possible by the comparison of the allopolyploid to the natural F1 hybrid species (*S. x townsendi*i, the progenitor of *S. anglica*) and *S. x neyrautii*, the other hybrid that has formed independently in southwest France (Baumel *et al.* 2003). MSAP data analysis revealed consistent methylation changes that contrast with the structural additivity of the parental genomes mentioned above. Most methylation changes were found in both *S. x townsendii* and *S. x neyrautii*, which indicates the reproducibility of the changes in the two different hybridisation events. The methylation alterations found in *S. anglica* were already present or initiated in *S. x townendii*, suggesting that epigenetic changes were triggered by hybridization rather than by genome duplication. The extent of such changes and their variability when plants are facing different environmental conditions need to be explored at the population level, and the sequences that are epigenetically affected have to be identified.

In the context of rapid expansion of invasive species that explore new habitats, epigenetic processes are of major interest as they definitely influence fitness. Because epigenetic cases of gene silencing will not be reflected in sequence data, the assessment of gene expression is key to the understanding of gene function and its importance in species adaptation and invasiveness. Molecular evolutionists are becoming more aware of the necessity to approach adaptive processes at both gene and genome levels.

## SELECTION, DEVELOPMENTAL RESPONSE, AND INVASIONS

Genetic change and subsequent alterations in developmental response have been minimally addressed in invasive plant species. Similarly, although the evaluation of developmental quantitative traits has been considered theoretically, there is little empirical evidence for or against their importance in plant invasions. The genetic and ecological interactions that result from changes in developmental genes or from genes of major effect could have profoundly complex repercussions. For example, the release from enemies may allow for decreased allocation to protective mechanisms and a concomitant increase in fitness that results from developmental responses. We know little about the ecological impacts of developmental changes and interactions in predator-prey relationships (Nijhout 2003). Action from just a few particularly important genes such as these may be key to the ability to invade (Paterson *et al.* 1995).

All adaptations important to invasiveness, *e.g.,* high seed production, breeding system changes, and vegetative propagation, are amenable for study in a developmental genetic and ecological context (Puragganan 2000, Gilbert and Bolker 2003). Genes such as *teosinte branched1* in maize illustrate the importance of developmental genes in plant establishment and spread (Q. Cronk pers. comm, Doebley *et al.* 1995). *Teosinte branched1*, which controls tillering in maize, is responsible for the difference between teosinte that is persistent in the environment, and varieties that are not ecologically competitive (Doebley *et al.* 1995). Variation in regulatory genes may be key to the provision of the genetic variation necessary to alter phenological developmental pathways, floral variation, secondary plant compound production, and clonal growth.

Life history strategies, often emphasized as key to understanding invasive ability have been illustrated as phenotypically environmentally dependent (Pigliucci 2001). The developmental response of reaction norms is based on mean phenotypic trait values, thus the variation must be explained by additive genetic variance or genes for “adaptive plasticity” (Sultan 2003). A comparison between *Polygonum* species with broad ecological tolerance to those limited by environmental factors demonstrate that developmental timing of plastic responses is important to environmental breadth (Sultan 2003). Gene expression is altered by both internal and more importantly, within the invasive species context, external cues (Schlichting 2003). Of particular importance to invasive ability may be the developmental plasticity of gender and breeding system flexibility which will impact sex ratios in propagules responding to new range environmental factors (Delph 2003). As Schaal *et al.* (2003) suggest, gene genealogies will be important to test hypotheses for adaptation, and we further suggest that this should include developmental traits that may be closely related to selection and adaptive divergence. Our expectation is that the phenomenon of rapid divergence of developmental traits will be found in other examples of island radiation or in regions similarly susceptible to invasion. In cases of gene duplication and polyploidy, the rate of this process may be increased, because of the “backup”genetic expression and copies with which selective processes can “tinker”.

## RESEARCH NEEDS IN THE AREA OF THE GENETICS AND EVOLUTION OF INVASIVE SPECIES

The distribution of genetic variation in populations of invasive species, and the relative invasiveness of different genotypes remains ellusive with few definitive studies outside of agricultural (but see Gaskin and Schaal 2002 and Saltonstall 2002). Of particular need in understanding the dynamics of adaptation and spread, is an assessment of the molecular population genetics of regulatory loci (Puragganan 2000).

Soil seedbank analysis as a source of new genetic variation has not been adequately addressed in plant invasions. Seed dormancy is an adaptive trait and although dormancy periods are well-described for many agricultural weeds (Baskin and Baskin 1998; Dekker 1997, 1999), virutally nothing is known about the importance of this trait for the maintainance of genetic diversity in invasive plant species. Seed viability for *Cytisus scoparius* can be as long as 60 years and a two- or three-year old plant can produce up to 18,000 seeds/year (Parker *et al.* 1994). Thus, gene flow from seed banks may be considerable. *Chromolaena odorata* (triffid weed), a shrub native to the neotropics and invasive throughout the Pacific Islands, is quite aggressive and even the occurrence of an occassional seedling six years past an irradication effort may be a potentially important source of genetic variation (Waterhouse and Zeimer 2000).

Quantitative trait loci analyses have proven to be very useful in agricultural genetics and there are numerous examples (Paterson 2002). In *Sorghum halepense*, variation in the number of rhizomes has been associated with three QTLs and the number of vegetative buds with an additional QTL (Paterson *et al.* 1995). The potential importance of this type of work can not be overstated; it has been well established that clonal growth and the ability to form more vegetative buds can be important to invasive ability (Paterson 2002). Continued work with agriculture species will aid the study of those genes that may be important in weediness such as floral or fruit regulation and vegetative growth. For example, the vegetative growth traits found in *S. halepense* correspond with the same QTLs in rice, wheat, corn, and likely other, but invasive, grasses. As so astutely noted by Paterson *et al.* (1995), QTL analysis can lead to the cloning of candidate genes important in vegetative growth. Once these genes are identified it may help in the specific eradication of some invaders that have large amounts of vegetative propagation through genetic or chemical methods.

Important contributions of the quantitative genetics in understanding invasive species evolution will result from studies which consider the adaptive response, or additive genetic variance of a particular trait (Lynch and Walsh 1998; Müller-Schärer and Steinger 2004). Such studies will be further strengthened by the identification of QTLs associated with these traits and their eventual molecular characterization. The integration of quantitative genetics and the molecular basis of these traits will eventually allow an assessment of the large-scale ecological effects of genetic traits.

As previously discussed, homeologous genes, or those genes duplicated by polyploid events, may undergo various evolutionary processes. Of particular interest are those genes that have adaptive significance. Specific questions that can be addressed to assess the dynamics of the genes in polyploid systems include: characterization in sequence and function between the different copies of the genes and in both the parental species and polyploid offspring; characterization of divergence times among the parental species and polyploid offspring.

Most importantly, the determination of the effects of polyploidy on duplicate gene expression and adaptive function is now possible. Much remains to be learned about the dynamics and subsequent genotypic and phenotypic changes due to the hybridization between historically allopatric taxa, homeologous genes, and allopolyploidization.

Although currently limited in their application to model systems or closely related taxa, the exploration of the use of new genomic tools, *e.g.*, microarrays may prove useful for the investigation of genomic and ecological interactions (Jackson *et al.* 2002).

## CONCLUSIONS

As evolutionary biologists, many of us have worked toward the day in which we can link gene and genomes to the level of the ecosystem. This day has arrived, and for better or worse, a forum that offers one of the best opportunities for the integration of genetics and ecology in an evolutionary context is the study of invasive species. Although the participants of the "genetics of colonizing species" symposium made this same observation in 1965; only now do we have the tools to address the myriad of questions associated with the evolution of invasive ability. We are well aware that it is perhaps more than a coincidence that many of the examples of invasive species we have cited often share the phenomena of rapid expansion into new ranges, polyploidy, and hybridization.

The integration of molecular genetics, ecology, and large-scale field experimentation is too large for any single investigator to study in invasive species or any other context. Increased knowledge in the respective fields of genomics, proteomics, cell biology, population genetics, phylogenetics, and ecology, will require the cooperation of laboratories with expertise in these respective areas. Perhaps invasive species genetics will be the field that brings together evolutionists from various disciplines for both a better understanding and the management of contemporary environments.

## ACKNOWLEDGEMENTS

We thank the National Science Foundation in the U.S.; the Centre National de la Recherche Scientifique, and the Centre Armoricain de Recherches en Environnement in France for their support of collaborative research on genome evolution of invasive plants. We also acknowledge and thank the contributions of our students and many collaborators to our work, particularly Norman Ellstrand. Curt Daehler and one anonymous reviewer are thanked for helpful comments on the manuscript.

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